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Review

Investigating the Crucial Role of Optic Flow in Postural Control: Central vs. Peripheral Visual Field

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Featured Application: In this paper, we performed a detailed review of different studies on the visual control of posture, which have led to controversial results. The specific applications of this review are (i) to critically analyze both the methodologies and the results of previous studies, (ii) to provide a general discussion of the state of the art in the field, and (iii) to provide readers with a discussion that could be helpful in preparing new methodological approaches for future experiments.

Abstract: Optic flow stimuli are crucial for the control of stance in the upright position. The visual control of posture has recently received a lot of interest from several researchers. One of the most intriguing aspects is the contribution of the different parts of the visual field in the control of stance. Here we reviewed the results of several studies performed with different methodologies that tried to determine the effect of optic flow on postural control, by analyzing the role of the central and peripheral visual fields. Although the results were controversial, the majority of these studies agreed to assign the most important role in postural control to the peripheral retina. However, these studies were performed using different approaches and different definitions of the central and peripheral visual fields. The choice of the exact portion of the retina to be stimulated is crucial given that the stimulation of the central and the peripheral parts of the retina leads to the activation of different geniculo-cortical pathways and results in different cortical processing of information.

Keywords: quiet stance; visual-motion processing; self-motion perception; body sway

1. Introduction

Different optic flow patterns provide important information about self-motion [1]. In 1950, James J. Gibson introduced the concept of "optic flow" to describe the visual stimulation provided to an observer who moves through the extra-personal space [2,3].

Within the cortical network, the optic flow input is integrated with other somato-sensory signals to guide locomotion and to maintain correct posture [4]. The somatosensory input originates from the proprioceptive signals of muscles and joints, whereas the vestibular input originates from the linear and rotational acceleration of the head relative to the body [5]. Optic flow is a complex visual array with specific spatial and temporal characteristics, like geometric structure, amplitude, speed, frequency, and location in the visual field (such as the foveal or peripheral regions). All these features can influence evoked postural responses [6–15]. The physiological mechanisms within the neural network integrate optic flow and other somato-sensory signals to generate a typical body oscillation, which has been called "body sway". Indeed, several studies have shown that visual stimulation evokes body sway [16–21]. These small postural oscillations reflect the regulatory activity of several control loops responsible for the control of posture [4,22].

It is known that in somato-sensory integration, the optic flow visual stimuli play a fundamental role in the maintenance of quiet stance in the upright position [11]. Changes in the visual input, such as passing from a dark to light environment, or directional changes such as from a forward to backward locomotion, require an updating of the sensory integration in order to provide the motor cortex with precise and consistent information about both the extra-personal space and the internal state [5,7,12,23]. Thus, a motor action consists of many interconnected contributing factors [11].

2. Optic Flow

The optic flow visual signal is created by the relative motion between an observer who moves through the environment and the environmental structures [2]. The extra-personal space consists of objects bounded by surfaces and visual perception is possible because light is reflected by such surfaces. In most cases, light is not reflected uniformly. Instead, it originates from a densely structured optical array at the point of observation. The optical array can be thought of as a bundle of narrow light cones, with their apices at the observation point [24]. Each cone has, as its basis, an element of distinct environmental texture and is therefore optically differentiable from its neighbors in terms of the intensity and the spectral composition of the light it contains. In each observation point there is a unique optical array. As a result, when the head or the eye moves relative to the environment, the optical array to the eye changes continuously over time, giving rise to an optical flow field.

Gibson showed that when an observer moves through the environment, the visual motion in the optical array expands radially from a single point, known as the "focus of expansion" (FOE), which has an important role in heading perception. The FOE is the point in the distance where the optic flow originates, thus in the FOE there is no flow. When an observer moves through the environment while fixating on his/her final destination, the visual perception of self-motion is mainly due to the FOE of the optic flow field. However, in daily life, self-motion perception requires the combination of different brain functions, given that eye and head movements change the FOE position with respect to the fovea.

The information provided by the optic flow input is necessary to encode the heading direction, spatial orientation and self-motion perception in the three-dimensional space [3,25]. Optic flow becomes absolutely important for the control of posture and locomotion, and for the selection of the appropriate motor actions [15,17,24,26]. Every transformation of the retinal input provides the observer with an experience of a movement. In the laboratory experimental condition, we usually have an immobile observer who views the optic flow stimuli projected on a screen. Thus, an expanding optic flow simulates a condition in which the observer moves forward, whereas a contracting optic flow simulates a condition in which the observer moves backward [27–35]. The processing of the perception of a movement is different in the retina, the brain or in the consciousness, because vision is a sensory-dependent variable of experience [2].

3. The Important Role of Optic Flow in Postural Control

In the last decade, the role of optic flow in the control of posture has received more and more interest from the scientific community and the research on many aspects has been advancing. Many factors have to be considered in the generation of the experimental paradigm, including the dimension of the stimulated visual field, the type of optic flow stimuli used (i.e., moving dots, moving stripes), and the duration of the stimulation.

This review focuses on an important aspect to take into account: the dimension of the stimulated visual field. The choice of the exact portion of the retina to be stimulated is crucial given that the stimulation of the different central and the peripheral parts of the retina leads to the activation of different geniculo-cortical pathways, which prompts different cortical processing of information, and thus results in a differential activation of motor pathways.

Until now, several studies have been aimed at uncovering the functional roles of the peripheral and central visual fields in postural control, leading to different conclusions. Many authors have

already pointed out that such differences and the controversial results are likely to have arisen from the different experimental protocols and approaches.

According to the retinal distribution of cone and rod photoreceptors, the definition of central vision ranges between 2° and 4° of the visual field [36]. In the retina, the density of the cone photoreceptors decreases as the distance from the fovea increases [37,38]. However, considering that projections from the retina to the cortical area are responsible for processing central vision, the central visual field has been defined as the 7° surrounding the fovea, thus including the foveal, parafoveal and perifoveal regions [39].

Besides the different definitions of the central and peripheral visual fields, the visual stimuli and the methodologies also differed across studies. In some studies, the stimuli were formed by random dot patterns, whereas in other studies, the stimuli were formed by vertical moving bars. In the majority of the studies, the stimuli were projected on a screen placed in front of the participants, whereas in other studies, the stimuli either originated from a side of the visual field or from placing subjects in a room with moving walls. The following chapters specify the protocols and definitions adopted by each study reported in this review, trying to explain how the different protocols conditioned the results.

3.1. The Functional Role of the Foveal and Peripheral Visual Field

In 1999, Bardy et al. summarized the various roles that have been ascribed to central and peripheral vision in perception and the control of self-motion [40]. The authors reported that three hypotheses have been postulated about the functional role of the foveal and peripheral visual field in the control of posture: (1) peripheral dominance, (2) retinal invariance, and (3) differential sensitivity to radial flow.

The peripheral dominance hypothesis states that peripheral vision is predominant for the perception of self-motion, while central vision is predominant for the perception of object-motion, meaning that the retinal position of the stimulus plays an important role in self-motion perception.

The retinal invariance hypothesis states that optic flow provides the necessary information to perceive both self-motion and object motion independent of the retinal stimulation locus. Thus, according to this view, there is no functional specialization for self-motion.

The functional sensitivity hypothesis states that the optic flow provides information for both self-motion and object-motion, but the central and peripheral parts of the retina are differentially sensitive to the optic flow patterns. According to this view, the central vision is more sensitive to radial, rotational, and lamellar optic flow patterns, while the peripheral vision is sensitive to lamellar optic flow, but insensitive to radial and rotational optic flow.

In the past two decades, many studies sought to uncover the functional differences between central and peripheral vision to determine which of these hypotheses was the most correct. Here we review those studies, trying to elucidate the reasons that led to such controversial results.

3.1.1. First Perspective: Peripheral Vision Plays the Most Important Role in Postural Control

The results of several papers seem to support the hypothesis that peripheral vision is more important than central vision in the control of posture. Amblard and Carblanc stimulated the participant's visual field (central and peripheral) with either a horizontal or a vertical rectangular grating. In their protocol, the lateral acceleration was measured at the level of the ankles, hips, and head. The results of their experiment showed that the peripheral vision played the most important role in postural control, while the central vision only played a supplementary role [41]. Berencsi et al. presented the participants with random patterns of circular dots that were either static or moving [42], showing that the peripheral vision had a stabilizing effect in the direction of the stimulus observation. These results suggested that peripheral vision makes a strong contribution to postural control, and that the peripheral visual field controlled posture in a head-centered rather than in a body-centered frame of reference. Kawakita et al. showed the participants random patterns of dots that were moving at a constant spatial frequency and were sinusoidal in depth [43]. The authors performed both central

and peripheral occlusions of the visual field to find that self-motion perception and body sway were more dependent on the stimulation of the peripheral visual field. Piponnier et al. examined the roles of central and peripheral vision in the control of posture by using a 3D tunnel stimulus that was either static or moving sinusoidally in the anterior–posterior direction [44]. The authors used peripheral and central occlusions at different degrees and a full visual field condition. In line with previous studies, the results showed that in the presence of an optic flow, the peripheral vision played a crucial role in postural control, being responsible for a compensatory sway, while central vision played an accessory role that was likely related to spatial orientation. Brandt et al. [6], using the simultaneous presentation of conflicting central and peripheral optokinetic stimuli, showed that the exocentric orientation was dependent on the peripheral stimuli. Previc and Neel examined how the size and eccentricity of a moving visual surround influenced the control of stance. Their results showed that postural control was determined primarily by visual motion in the peripheral visual field [45]. Raffi et al., using a set of visual stimuli made by expanding and contracting optic flow patterns, showed that the visual stimuli always evoked an excitatory input on postural muscles, but that the stimulus structures produced different postural effects [21]. The authors found that the stimuli presented in the peripheral visual field stabilized body sway, while stimuli presented in the central visual field evoked much larger body sways. In a recent study, Horiuchi et al. manipulated the central and peripheral visual fields and the occurrence of optical flow during quiet standing [46]. The results showed that stimuli presented in the peripheral visual field evoked smaller postural sway than stimuli presented in the central visual field, meaning that the optical flow occurring in the peripheral visual field was essential for stable quiet standing.

3.1.2. Second Perspective: Central and Peripheral Vision have the Same Functional Role

Straube et al. carried out an interesting experiment in 1994 [47]. The authors performed occlusions of some parts of the visual field by attaching blinds to a helmet worn by the participants. When the authors stimulated peripheral and central visual fields to the same extent, the postural sway was smaller with central vision. However, if the peripheral field of stimulation was corrected by the cortical magnification factor of the retina in the primary visual cortex such that there was a correspondence between retinal and cortical activity, no difference in the stabilizing effect was found between peripheral and central vision. Thus, according to the results of this experiment, there was no functional specialization of peripheral and central vision in postural control. These results suggested that visual stabilization of quiet stance was a function of the field size and cortical representation of the retina.

3.1.3. Third Perspective: Central and Peripheral Vision Have Functional Differences and Complementary Roles

The study by Andersen and Braunstein in 1985 examined the importance of the stimulation area in the central visual field, by using radial expansion dot patterns with different visual angles [48]. The results suggested that in addition to the specific information processing system that was required for peripheral vision, there was a higher-level system that used information from complex stimuli in the central visual field. Stoffregen in 1985 examined the importance of the central and peripheral visual fields in the control of stance, as a function of the geometrical structure of the optic flow field [12]. Stoffregen performed the experiments in a moving room to measure the magnitude of the compensatory sway in response to movements of the room. When radial optic flow was presented in the peripheral retina, no compensatory sway was found, while some body oscillation was found when lamellar flow was presented in the central field. This result suggested that the optic flow structure interacted with the stimulated retinal area in the control of stance. In 1988, van Asten et al. investigated how the optic flow input affected postural readjustments [15]. The authors found that the amplitude of the postural responses did not depend on the magnitude of the optic flow components and that the peripheral visual field did not have an exclusive role in the control of postural sway. Nougier et al. [49]

showed that both peripheral and central vision contributed equally to children's postural stability at ages 6 and 10. However, at age 8, central vision was more efficient in stabilizing posture. The authors stated that the contribution of central and peripheral visual fields to postural control depended on age and was as a function of the plane of body oscillations.

3.2. Different Methodologies Used for Assessing the Role of the Central and Peripheral Visual Fields

As introduced earlier, several studies aimed at uncovering the functional roles of the peripheral and central visual fields in postural control have reached different conclusions. According to the retinal distribution of photoreceptors, the definition of central vision ranges between 2° and 4° of the visual field [36]. However, considering the projections from the retina to the cortical visual areas, the central visual field has been defined as the 7° of the regions surrounding the fovea [39]. It has to be noted that the few papers that aimed at investigating the role of central vision used stimuli whose dimensions ranged from 7° to 60°. Berencsi et al. stimulated the central visual field with stimuli of 4° and 7° [42]; Raffi et al. used stimuli of 7° [18,21]; Horiuchi et al. used stimuli of 8° [46]; Nougier et al. used stimuli of 10° [49]; Previc and Neel used stimuli that ranged from 15° to 60° [45]; and Piponnier et al. used stimuli that ranged from 4° to 30° [44].

The peripheral visual field is commonly considered to be the area adjacent to the central visual field. Thus, if the central visual field was not uniformly defined, the peripheral visual field would also be affected by the same issue. For this reason, Raffi et al. [18,21] considered the periphery of the visual field outside the inner 20° of the central visual field, to ensure stimulation of a retinal region formed only by rod photoreceptors [50].

Besides the different definitions of central and peripheral visual fields, the methodologies and the visual stimuli also differed between the studies. In few studies, stimuli were formed by random patterns of dots which only provided spatiotemporal changes in the visual field [42]. In other studies, stimuli were made of patterns of vertical or horizontal bands that alternated between black and white [41]. Undoubtedly, the use of different moving visual stimuli and/or the different retinal area of stimulation changed the evoked muscular responses. Stoffregen et al. [12,14] stimulated the central visual field by presenting moving stimuli in front of the subjects, while stimulating the peripheral visual field by presenting moving stimuli to the right and left of the subjects. As Horiuchi [46] already pointed out, this type of stimulation might not be adequate for studying the functional role of the peripheral and central visual fields given that the dimensions of the stimulated visual field varied significantly and were not directly changed. Other authors used an occlusion method in their stimulation paradigm, which resulted in a more specific distinction between the stimulated retinal areas [18,21,42,43,46]. Table 1 reports the fundamental aspects of each paper including methodologies and conclusions.

Table 1. Comparison of methodologies and definition criteria across studies.

	Central	Peripheral	Type of Stimuli	Protocol	Conclusions
Andersen and Braunstein, 1985	7–21°	7–21°	Random dots	Stimuli projected on a screen; stimuli translated along the line of sight	Central and peripheral field have complementary roles
Berencsi et al. 2005	4–7°	Area adjacent to central field; Central field occluded	Random dots	Stimuli projected on a screen	Major role of periphery
Brandt et al. 1973	Up to 30°	Central occlusion up to 120°	Optokinetic stimuli	Rotating chair; wall painted with b/w stripes	Major role of periphery
Horiuchi et al. 2017	8°	Area adjacent to central	Random dots	Stimuli projected on a screen or goggles	Major role of periphery
Kawakita et al. 2000	14–33°	Area adjacent to central field; central field occluded	Random dots	Stimuli projected on a screen	Major role of periphery
Nougier et al. 1998	10°	Area outside 20° of central occlusion	Environmental stimuli	Use of goggles	Central and peripheral field have complementary roles
Piponnier et al. 2009	4–30°	Area adjacent to central field; central field occluded	3D tunnel static or moving AP	Subject in a virtual environment	Major role of periphery
Previc and Neel 1995	15–60°	60–110°	Small squares	Virtual rotating surrounds	Major role of periphery
Raffi et al. 2014	7°	Area outside 20° of central occlusion	Random dots	Stimuli projected on a screen	Major role of periphery
Stoffregen 1985	20–60°	Stimulus projected from the side of the subject	Environmental stimuli	Stimuli projected in front of a screen for central, on the side for the periphery	Central and peripheral field have complementary roles
Straube et al. 1994	1–8°	10–30° of retinal eccentricity	Environmental stimuli	Subjects standings	Central and peripheral field have the same functional role
Van Asten et al. 1988	Up to 15°	Central occlusion of 15 × 30°	Black and white patterns	Stimuli projected on a screen simulating motion through a tunnel or along a wall	Central and peripheral field have complementary roles

4. Visual Pathways

Uncovering the role of optic flow in postural control, and more specifically, elucidating the functional differences between the central and peripheral visual fields, is challenging due to the complex anatomo-physiological organization of the mammalian retina. Anatomical studies showed that each retinal area projects to different cortical pathways. It is thought that the primate retina contains more than 20 types of ganglion cells, most of which are unstudied. Dannis Dacey reported that there are three main types of ganglion cells projecting to the lateral geniculate nucleus: the parasol, the midget and the small bistratified cells [51]. As reported by Dacey in 1994, the relative densities of the three types of ganglion cells vary in eccentricity. In the fovea, the midget cells represent about 90% of the total ganglion cells, the parasol cells about 5% and small bistratified cells about 1%. On the contrary, the peripheral retina is formed for the major part by the midget cells, which are the 45–50% of the total ganglion cells, the parasol cells are about 20% and the small bistratified cells are about 10%. Thus, from the peripheral to the central retina, the number of midget ganglion cells progressively increases relative to the parasol and the small bistratified types [51]. The parasol cells project to the geniculate magnocellular layers while the midget and the bistratified cells project to the geniculate parvocellular layers.

In the lateral geniculate nucleus, the parvocellular and magnocellular layers originate from two different pathways, namely the ventral and dorsal visual streams, respectively. The ventral stream, which mostly originates from the fovea, processes information related to the color and shape of objects; it is also called the "what" pathway. On the other hand, the dorsal stream, which mostly originates from the peripheral regions of the retina, processes information related to self-motion perception, depth, and spatial orientation; it is also called the "where" pathway [52–55].

Dearing and Harris already reported that the view that the peripheral visual field is crucial in generating vection has been challenged [56]. A reasonable behavioral explanation for the periphery being more important in perceptual orientation arises from the observation that the peripheral visual field is not usually occluded by objects of interest. In addition, salient features that are relevant for motion perception, like walls or floors, are more visible in this region.

It thus becomes clear that a precise anatomical distinction between the foveal (or central) and peripheral retinal fields is necessary for developing an appropriate experimental protocol to study the contribution of optic flow in postural control. Even the inclusion of a few degrees of visual angle in either the peripheral or central visual fields could change the results and lead to contradictory findings.

5. Conclusions

It has to be noted that the majority of studies recognized the greater role of the peripheral field in controlling body sway, however, some notable experiments pointed out that there could be a complex interaction between the central and peripheral visual fields [12,14,15,56]. On the basis of these results and on the anatomo-physiological organization of the visual system, it is possible to hypothesize that the peripheral visual field may play the most important role, while interacting with the central visual field for processing, and contributing to factors like visual acuity [57]. Future experiments aimed at uncovering the functional differences between the two parts of the visual field should be designed, paying particular attention to (i) the anatomical boundaries of the central field of view, (ii) the participants' attentional demands, trying to avoid a shift in the participants' attention during the task execution, and (iii) the potential execution of eye movements by trying to avoid a refresh of the visual scene that could alter the cortical input.

Selection of the Studies: The discussed studies were selected following these steps: (1) previous knowledge of the studies, (2) search by keywords in various database (Pubmed, Scopus, and Google Scholar); keywords: central, peripheral, posture, stance, visual perception, (3) citation of past relevant papers and book chapters. The criteria for exclusion were: (1) studies performed on subjects with pathologies or retinal dysfunction, (2) studies performed on elderly subjects, (3) studies non-specifically related at uncovering the functional difference between central and peripheral visual field.

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References

1. Lappe, M.; Bremmer, F.; van den Berg, A.V. Perception of self-motion from visual flow. *Trends Cogn. Sci.* **1999**, *3*, 329–336. [CrossRef]
2. Gibson, J.J. *The Perception of the Visual World*; Houghton Mifflin: Boston, MA, USA, 1950.
3. Gibson, J.J. The visual perception of objective motion and subjective movement. *Psychol. Rev.* **1954**, *61*, 304–314. [CrossRef] [PubMed]
4. Peterka, R.J.; Benolken, M.S. Role of somatosensory and vestibular cues in attenuating visually induced human postural sway. *Exp. Brain Res.* **1995**, *105*, 101–110. [CrossRef] [PubMed]
5. Yamada, M.; Higuchi, T.; Mori, S.; Uemura, K.; Nagai, K.; Aoyama, T.; Ichihashi, N. Maladaptive turning and gaze behavior induces impaired stepping on multiple footfall targets during gait in older individuals who are at high risk of falling. *Arch. Gerontol. Geriatr.* **2012**, *54*, e102–e108. [CrossRef] [PubMed]
6. Brandt, T.; Dichgans, J.; Koenig, E. Differential effects of central versus peripheral vision on egocentric and exocentric motion perception. *Exp. Brain Res.* **1973**, *16*, 476–491. [CrossRef] [PubMed]
7. Dijkstra, T.M.; Schöner, G.; Gielen, C.C. Temporal stability of the action-perception cycle for postural control in a moving visual environment. *Exp. Brain Res.* **1994**, *97*, 477–486. [CrossRef] [PubMed]
8. Dijkstra, T.M.; Schöner, G.; Giese, M.A.; Gielen, C.C.A.M. Frequency dependence of the action-perception cycle for postural control in a moving visual environment: Relative phase dynamics. *Biol. Cybern.* **1994**, *71*, 489–501. [CrossRef] [PubMed]
9. Kiemel, T.; Oie, K.S.; Jeka, J.J. Multisensory fusion and the stochastic structure of postural sway. *Biol. Cybern.* **2002**, *87*, 262–277. [CrossRef] [PubMed]
10. Lestienne, F.; Soechting, J.; Berthoz, A. Postural readjustments induced by linear motion of visual scenes. *Exp. Brain Res.* **1977**, *28*, 363–384. [CrossRef] [PubMed]
11. Peterka, R.J. Sensorimotor integration in human postural control. *J. Neurophysiol.* **2002**, *88*, 1097–1118. [CrossRef] [PubMed]
12. Stoffregen, T.A. Flow structure versus retinal location in the optical control of stance. *J. Exp. Psychol. Hum. Percept. Perform.* **1985**, *11*, 554–565. [CrossRef] [PubMed]
13. Stoffregen, T.A. The role of optical velocity in the control of stance. *Percept. Psychophys.* **1986**, *39*, 355–360. [CrossRef] [PubMed]
14. Stoffregen, T.A.; Schmuckler, M.A.; Gibson, E.J. Use of central and peripheral optic flow in stance and locomotion in young walkers. *Perception* **1987**, *16*, 113–119. [CrossRef] [PubMed]
15. Van Asten, W.N.; Gielen, C.C.; van der Gon, J.J.D. Postural adjustments induced by simulated motion of differently structured environments. *Exp. Brain Res.* **1988**, *73*, 371–383. [CrossRef] [PubMed]
16. Bronstein, A.M. Suppression of visually evoked postural responses. *Exp. Brain Res.* **1986**, *63*, 655–658. [CrossRef] [PubMed]
17. Lee, D.; Lishman, J.R. Visual proprioceptive control of stance. *J. Hum. Mov. Stud.* **1975**, *1*, 87–95.
18. Persiani, M.; Piras, A.; Squatrito, S.; Raffi, M. Laterality of stance during optic flow stimulation in male and female young adults. *BioMed Res. Int.* **2015**, *2015*, 542645. [CrossRef] [PubMed]
19. Piras, A.; Raffi, M.; Perazzolo, M.; Squatrito, S. Influence of heading perception in the control of posture. *J. Electromyogr. Kinesiol.* **2018**, *39*, 89–94. [CrossRef] [PubMed]
20. Raffi, M.; Piras, A.; Persiani, M.; Perazzolo, M.; Squatrito, S. Angle of gaze and optic flow direction modulate body sway. *J. Electromyogr. Kinesiol.* **2017**, *35*, 61–68. [CrossRef] [PubMed]
21. Raffi, M.; Piras, A.; Persiani, M.; Squatrito, S. Importance of optic flow for postural stability of male and female young adults. *Eur. J. Appl. Physiol.* **2014**, *114*, 71–83. [CrossRef] [PubMed]
22. Collins, J.J.; de Luca, C.J. The effects of visual input on open-loop and closed-loop postural control mechanisms. *Exp. Brain Res.* **1995**, *103*, 151–163. [CrossRef] [PubMed]
23. Martin, O.; Gascuel, J.D. Reactive Ocular and Balance Control in Immersive Visual Flows: 2D vs. 3D Virtual Stimuli. *Stud. Health Technol. Inform.* **2009**, *144*, 208–210. [PubMed]
24. Lee, D.N. The optic flow field: The foundation of vision. *Phil. Trans. R. Soc. Lond. B* **1980**, *290*, 169–179. [CrossRef] [PubMed]

25. Gibson, J.J. Visually controlled locomotion and visual orientation in animals. *Br. J. Psychol.* **1958**, *49*, 182–194. [CrossRef] [PubMed]
26. Lee, D.N.; Craig, C.M.; Grealy, M.A. Sensory and intrinsic coordination of movement. *Proc. R. Soc. B Biol. Sci.* **1999**, *266*, 2029–2035. [CrossRef] [PubMed]
27. Duffy, C.J.; Wurtz, R.H. Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large field stimuli. *J. Neurophysiol.* **1991**, *65*, 1329–1345. [CrossRef] [PubMed]
28. Duffy, C.J.; Wurtz, R.H. Sensitivity of MST neurons to optic flow stimuli. II. Mechanism of response selectivity revealed by small-field stimuli. *J. Neurophysiol.* **1991**, *65*, 1346–1359. [CrossRef] [PubMed]
29. Raffi, M.; Carrozzini, C.; Maioli, M.G.; Squatrito, S. Multimodal representation of optic flow in area PEc of macaque monkey. *Neuroscience* **2010**, *171*, 1241–1255. [CrossRef] [PubMed]
30. Raffi, M.; Maioli, M.G.; Squatrito, S. Optic flow direction coding in area PEc of the behaving monkey. *Neuroscience* **2011**, *194*, 136–149. [CrossRef] [PubMed]
31. Raffi, M.; Persiani, M.; Piras, A.; Squatrito, S. Optic flow neurons in area PEc integrate eye and head position signals. *Neurosci. Lett.* **2014**, *568*, 23–28. [CrossRef] [PubMed]
32. Raffi, M.; Piras, A.; Calzavara, R.; Squatrito, S. Area PEc Neurons Use a Multiphasic Pattern of Activity to Signal the Spatial Properties of Optic Flow. *BioMed Res. Int.* **2017**, *2017*, 6495872. [CrossRef] [PubMed]
33. Raffi, M.; Siegel, R.M. A functional architecture of optic flow in the inferior parietal lobule of the behaving monkey. *PLoS ONE* **2007**, *2*, e200. [CrossRef] [PubMed]
34. Raffi, M.; Squatrito, S.; Maioli, M.G. Neuronal responses to optic flow in the monkey parietal area PEc. *Cereb. Cortex* **2002**, *12*, 639–646. [CrossRef] [PubMed]
35. Siegel, R.M.; Read, H.L. Analysis of optic flow in the monkey parietal area 7a. *Cereb. Cortex* **1997**, *7*, 327–346. [CrossRef] [PubMed]
36. Osaka, N. Peripheral Vision. In *New Sensation Perception Psychology Handbook*; Oyama, T., Imai, S., Wake, T., Eds.; Seishin-Shobou: Tokyo, Japan, 1994; pp. 923–930.
37. Curcio, C.A.; Sloan, K.R.; Kalina, R.E.; Hendrickson, A.E. Human photoreceptor topography. *J. Comp. Neurol.* **1990**, *292*, 497–523. [CrossRef] [PubMed]
38. Curcio, C.A.; Sloan, K.R.; Packer, O.; Hendrickson, A.E.; Kalina, R.E. Distribution of cones in human and monkey retina: Individual variability and radial asymmetry. *Science* **1987**, *236*, 579–582. [CrossRef] [PubMed]
39. Mishkin, M.; Ungerleider, L.G. Contribution of striate inputs to the visuospatial functions of parietopreoccipital cortex in monkeys. *Behav. Brain Res.* **1982**, *6*, 57–77. [CrossRef]
40. Bardy, B.G.; Warren, W.H.J.; Kay, B.A. The role of central and peripheral vision in postural control during walking. *Percept. Psychophys.* **1999**, *61*, 1356–1368. [CrossRef] [PubMed]
41. Amblard, B.; Carblanc, A. Role of foveal and peripheral visual information in maintenance of postural equilibrium in man. *Percept. Mot. Ski.* **1980**, *51*, 903–912. [CrossRef] [PubMed]
42. Berencsi, A.; Ishihara, M.; Imanaka, K. The functional role of central and peripheral vision in the control of posture. *Hum. Mov. Sci.* **2005**, *24*, 689–709. [CrossRef] [PubMed]
43. Kawakita, T.; Kuno, S.; Miyake, Y.; Watanabe, S. Body sway induced by depth linear vection in reference to central and peripheral visual field. *Jpn. J. Physiol.* **2000**, *50*, 315–321. [CrossRef] [PubMed]
44. Piponnier, J.C.; Hanssens, J.M.; Faubert, J. Effect of visual field locus and oscillation frequencies on posture control in an ecological environment. *J. Vis.* **2009**, *9*, 1–10. [CrossRef] [PubMed]
45. Previc, F.H.; Neel, R.L. The effects of visual surround eccentricity and size on manual and postural control. *J. Vestib. Res.* **1995**, *5*, 399–404. [CrossRef]
46. Horiuchi, K.; Ishihara, M.; Imanaka, K. The essential role of optical flow in the peripheral visual field for stable quiet standing: Evidence from the use of a head-mounted display. *PLoS ONE* **2017**, *12*, e0184552. [CrossRef] [PubMed]
47. Straube, A.; Krafczyk, S.; Paulus, W.; Brandt, T. Dependence of visual stabilization of postural sway on the cortical magnification factor of restricted visual fields. *Exp. Brain Res.* **1994**, *99*, 501–506. [CrossRef] [PubMed]
48. Andersen, G.J.; Braunstein, M.L. Induced self-motion in central vision. *J. Exp. Psychol. Hum. Percept. Perform.* **1985**, *11*, 122–132. [CrossRef] [PubMed]
49. Nougier, V.; Bard, C.; Fleury, M.; Teasdale, N. Contribution of central and peripheral vision to the regulation of stance: Developmental aspects. *J. Exp. Child Psychol.* **1998**, *68*, 202–215. [CrossRef] [PubMed]

50. Osterberg, G. Topography of the layer of rods and cones in the human retina. *Acta Ophthal.* **1935**, *13* (Suppl. 6), 11–97.
51. Dacey, D.M. Physiology, morphology and spatial densities of identified ganglion cell types in primate retina. *Ciba Found. Symp.* **1994**, *184*, 12–28. [PubMed]
52. Gattass, R.; Rosa, M.G.; Sousa, A.P.; Pinon, M.C.; Fiorani, M.J.; Neuenschwander, S. Cortical streams of visual information processing in primates. *Braz. J. Med. Biol. Res.* **1990**, *23*, 375–393. [PubMed]
53. Goodale, M.A.; Milner, A.D. Separate visual pathways for perception and action. *Trends Neurosci.* **1992**, *15*, 20–25. [CrossRef]
54. Ungerleider, L.G.; Haxby, J.V. 'What' and 'where' in the human brain. *Curr. Opin. Neurobiol.* **1994**, *4*, 157–165. [CrossRef]
55. Ungerleider, L.G.; Mishkin, M. Two cortical visual systems. In *Analysis of Visual Behaviour*; Ingle, D.J., Goodale, M.A., Mansfield, R.J.W., Eds.; MIT Press: Cambridge, MA, USA, 1982.
56. Dearing, R.R.; Harris, L.R. The contribution of different parts of the visual field to the perception of upright. *Vis. Res.* **2011**, *51*, 2207–2215. [CrossRef] [PubMed]
57. Uchiyama, M.; Demura, S. Low visual acuity is associated with the decrease in postural sway. *Tohoku J. Exp. Med.* **2008**, *216*, 277–285. [CrossRef] [PubMed]